Larval Development of *Ceratitis capitata* (Diptera: Tephritidae) on a Meridic Diet

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ABSTRACT A meridic diet (*Ceratitis capitata* #1) containing corncob as a bulking agent was developed and found comparable to diets currently used for rearing the larvae of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). The composition of *C. capitata* #1 diet (mg/50 g diet) is essential amino acids 636; arginine, 106.8; histidine, 45.6; isoleucine, 56.4; leucine, 108; lysine, 58.8; methionine, 27.6; phenylalanine, 70.8; threonine, 54; tryptophan, 28.8; valine, 79.2; non-essential amino acids 964.8; alanine, 78; aspartic acid, 112.8; cystine, 40.8; glutamic acid, 392.4; glycine, 90; proline, 124.8; serine, 78; tyrosine, 48; ribonucleic acid, 100; vitamins, 5.35; (thiamine [vitamin B_1], 1.0; riboflavin [vitamin B_2], 1.0; nicotinic acid, 1.0; pantothenic acid, 1.0; pyridoxine [vitamin B_6], 1.0; biotin, 0.1; folic acid, 0.25); anti-microbials, 256 (methylparaben), 100; sodium benzoate, 100; p-amino benzoic acid, 1.0; streptomycin, 50; oxytetracycline, HCl 5; cholesterol, 40; inositol, 10; choline chloride, 20; minerals (McCollum and Davis Salt mixture No. 185), 100; citric acid (acidulant), 500; sucrose, 2000; corncob grit (screen size 30/80), 12,000; distilled water, 33,000 and pH 3.5. The omission of all 10 essential amino acids from the meridic diet mixture inhibited development past the first instar. Deletion of eight non-essential amino acids, 10 vitamins, sugar, or ribonucleic acid delayed larval growth. In addition, larvae reared on diet without non-essential amino acids, vitamins, sugar or cholesterol resulted in pupal weight loss. Pupal recovery and adult emergence were affected by the removal of 10 vitamins or cholesterol from the *C. capitata* #1 diet. Flight ability was decreased in the absence of 10 vitamins. No significant effects were shown in diet lacking salt mixture.

KEY WORDS *Ceratitis capitata*, meridic diet, mass rearing

THE LARVAE OF the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), have been reared for sterile-insect technique programs on a variety of artificial diets for decades. Available information on larval nutritional requirements for tephritids stems from the search for crude diet ingredients that improve survival, growth, or development and the utilization of dry plant materials or dry yeasts to improve diet texture and nutrition (Marlowe 1934; Christenson et al. 1956; Schroeder et al. 1971, 1972; Zumreoglu et al. 1979; Vargas et al. 1983, 1993, 1994; Andres and Muniz 1984; Vargas and Mitchell 1987; Chan et al. 1990; Manoukas and Zografou 1997; Moreno et al. 1997; Saldanha and Silva 1999). Information on nutrients needed for tephritids, especially *C. capitata* larvae, is very limited (Srivastava and Pant 1981; Zucoloto 1987; Kanthi and Pant 1988; Achala-Paripurna and Srivastava 1989; Zucoloto 1991; Kumar and Anand 1992; Lemos et al. 1992).

The larval diet currently used for mass rearing in Hawaii is slightly modified from that developed by Tanaka et al. (1969) and consists of 11.13% sugar, 3.11% torula yeast, 0.2% sodium benzoate, 0.2% methylparaben, 0.13% streptomycin, 0.01% oxytetracycline HCl, 2.11% citric acid, 59.11% water, and 24% millfeed as a bulking agent. The nutrients from these diet ingredients apparently are sufficient to support larval development. However, for optimization of growth and development, a completely chemically defined diet is a necessity to gain a better understanding of nutritional requirements for *C. capitata.* This article describes the composition of a meridic diet (containing at least one unknown chemical structure) and the suitability of this meridic diet for the larval development of *C. capitata.* This meridic diet provides the baseline nutrient information for our development of a completely chemically defined diet.

Materials and Methods

Insects. Eggs of *C. capitata* were obtained from adult colonies of the Maui Med-93 strain maintained at U.S. Pacific Basin Agricultural Research Center (USPBARC), USDA-ARS, Honolulu, HI. This colony has been reared for ≈60 generations on a modified diet of Tanaka et al. (1969) (diet T; Table 1). Newly hatched larvae (within 12 h) were used as the starting stage for bioassay throughout this study.

Diets. All chemicals were purchased from ICN Biomedicals (Costa Mesa, CA). The agar diet (diet S; Table 1), originally developed by Srivastava et al. (1989) for *Bactrocera dorsalis* (Hendel), was used as a model diet. I replaced agar with corncob (30/80 grit size, Mt. Pulaski Products, IL) and casein with purified amino acids included in millfeed to produce the *C. capitata* #1 meridic diet. The composition and formu-

Table 1. Composition (mg per 50 g diet) of modified Tanaka diet (diet T), Srivastava casein diet (diet S) and *C. capitata* #1 meridic diet

Constituents	Diet T	Diet S	*C. capitata* #1 diet
Amino acid mixture	—	—	1,600.80
Casein (vitamin free)	—	3,500.00	—
Torula yeast	1,550.00	—	—
Ribonucleic acid	—	100.00	100.00
Sugar	5,500.00	2,000.00	2,000.00
Cholesterol	—	40.00	40.00
Vitamin mixture	—	36.35	36.35
McCollum & Davis Salt mixture No. 185	—	100.00	100.00
Streptomycin	50.00	—	50.00
Oxytetracycline HCL	5.00	—	5.00
Chloram phenicol	—	100.00	—
Methylparaben	100.00	100.00	100.00
Sodium benzoate	100.00	—	100.00
Potassium hydroxide 10%	—	0.40	—
Citric acid	1,550.00	—	500.00
Corncob 30/80	—	—	12,000.00
Millfeed	12,000.00	—	—
Agar	—	1,000.00	—
Water	29,500.00	40,000.00	33,000.00

lation of this diet are listed in Tables 1 and 2. Diet T was used as a control diet.

In general, all diets were prepared as follows: A mixture of 18 amino acids and the vitamin mixture were each prepared in bulk (Table 2). They were combined with other ingredients—sugar, McCollum and Davis (Aurora, OH) salt mixture No. 185, cholesterol, methylparaben, sodium benzoate, streptomycin, oxytetracycline HCl, citric acid, and ribonucleic acid. All dry materials (including 12 g of corncob bulking agent) were weighed into sterile polyethylene Stomacher blender bags (80 ml, 16 by 10 cm) and mixed in a Stomacher laboratory blender (400 ml capacity) (Daigger and Company, Lincolnshire, IL) at the normal setting for 60 s. Hot water (55°C; 33 ml) was then added into this diet mixture and mixed in the Stomacher blender for an additional 120 s at high speed. Diet mixtures in the sampling bags were labeled and stored in a refrigerator (4°C) for later use. Before use, diets were taken from refrigeration to a room kept at 24 ± 1°C and 65 ± 1% RH, where the diets were mixed at a normal setting for 60 s.

Bioassays. Fifty newly eclosed larvae were randomly selected from 1 ml of eggs and were transferred onto a strip of blotting paper on top of 50 g of diet inside a sterile polyethylene bag using a fine brush. Four bags of each test diet were prepared individually. Each bag was stapled on the creases of the bag and maintained at 24 ± 1°C and 65 ± 1% RH. When larvae reached third instar, polyethylene bags were opened and placed in a one-liter waxed cup with vermiculite for pupation. Pupae were counted and weighed as soon as brown puparia were formed. Pupae recovered from each diet were expressed as percent recovery of neonate larvae used. Daily pupal weights were totaled and divided by the total number of pupae from each diet to calculate mean pupal weight. The larval development period was measured from egg hatch to the first day of pupation. The mean larval developmental period was calculated by using a weighed arithmetic mean—the sum of the daily pupal collections times the number of days to pupation divided by total number of pupae (Sanders 1990). Adult emergence and flight ability were determined according to Boller et al. (1981) and Chang et al. (2000). Percent fliers were derived from the total number of pupae minus the number of unemerged, partially emerged, emerged but deformed, and nonfliers divided by the total number of emerged flies and multiplied by 100. Each test was repeated four times. Four batches of emerged adults from each test were combined and placed in a metal cage (26.5 by 26.5 by 26.5 cm) for egg collection. Eggs were collected when adults were 6 d old and continued for four consecutive days. Four hundred eggs per diet per day were transferred into four strips of blotting papers (100 eggs each) inside a petri dish for egg hatch. Percent egg hatch was calculated as mean number of larvae eclosed from each 100 eggs times 100.

A deletion technique was used to determine the importance of nutrients in *C. capitata* #1 diet. Groups

Table 2. Composition of *C. capitata* #1 diet

Constituents	(mg/50 g diet)
Amino acids	1,600.8
Essential amino acids	636.0
L-arginine	106.8
L-histidine	45.6
L-isoleucine	56.4
L-leucine	108.0
L-lysine	58.8
L-methionine	27.6
L-phenylalanine	70.8
L-threonine	54.0
L-tryptophan	28.8
L-valine	79.2
Non-essential amino acid	964.8
L-alanine	78.0
L-aspartic acid	112.8
L-cysteine	40.8
L-glutamic acid	392.4
L-glycine	90.0
L-proline	124.8
L-serine	78.0
L-tyrosine	48.0
Vitamins	36.35
Thiamin (Vit. B_1)	1.00
Riboflavin (Vit. B_2)	1.00
Nicotinic acid	1.00
Pantothenic acid (Coenzyme A)	1.00
Pyridoxine (Vit. B_6)	1.00
Folic acid	0.25
Biotin	0.10
Inositol	10.00
Choline chloride	20.00
p-amino benzoic acid	1.00
Ribonucleic acid	100.00
Sugar	2,000.00
Cholesterol	40.00
McCollum & Davis Salt mixture No. 185	100.00
Streptomycin	50.00
Oxytetracycline HCL	5.00
Methylparaben	100.00
Sodium benzoate	100.00
Citric acid	500.00
Corncob 30/80	12,000.00
Distilled Water	33,000.00

Table 3. Comparison of *C. capitata* #1 larval diet and currently used mass rearing control diet (diet T) over two generations

	Larval period, days	% pupal recovery	Pupal wt, mg	% adult emergence	Flier, %	Egg hatch, %
Control (P)	8.13 ± 0.04c	95.00 ± 2.08a	9.55 ± 0.09b	96.85 ± 1.03a	39.48 ± 8.23a	95.00 ± 0.58a
C. capitata #1 (P)	9.47 ± 0.08a	93.00 ± 1.29a	9.52 ± 0.17b	92.95 ± 1.91a	45.29 ± 3.33a	94.38 ± 0.97a
Control (F_1)	7.52 ± 0.06d	93.00 ± 3.00a	10.48 ± 0.11a	95.13 ± 0.61a	37.83 ± 7.04a	93.94 ± 0.72a
C. capitata #1 (F_1)	8.81 ± 0.16b	92.50 ± 4.86a	9.98 ± 0.15ab	97.98 ± 1.17a	64.32 ± 5.49a	92.38 ± 0.73a
Control (F_2)	7.49 ± 0.03d	89.50 ± 1.71a	10.48 ± 0.11a	97.24 ± 1.63a	51.30 ± 3.77a	95.06 ± 0.90a
C. capitata #1 (F_2)	8.60 ± 0.08b	89.50 ± 1.50a	10.48 ± 0.03a	92.04 ± 2.80a	57.65 ± 6.07a	91.50 ± 1.14a
F value	77.60	0.65	14.97	2.09	3.11	2.88
df	18	18	18	18	18	18
P	<0.0001	0.6650	<0.0001	0.1137	0.0338	0.0185

Means within a column followed by different letters were statistically different ($\alpha = 0.05$, ANOVA test).

of nutrients (either essential amino acids, non-essential amino acids, or vitamins) or individual nutrients (sugar, cholesterol, salt mixture, or ribonucleic acid) were systematically deleted from *C. capitata* #1 meridic diet, and the importance of these nutrients in the diet was evaluated. In addition, larvae were reared on *C. capitata* #1 diet for two subsequent generations (F_1 and F_2) following the parental generation to evaluate the quality of fruit flies fed on the *C. capitata* #1 diet.

Statistical Analysis. Data are reported as means ± SE. Differences among means were determined by analysis of variance (ANOVA), with the honestly significant difference (HSD) value calculated as Tukey's statistic at $\alpha = 0.05$ (SAS Institute 1996).

Results and Discussion

Diet Development. Our initial approach to develop this diet was using Srivastava casein larval diet for *B. dorsalis* (diet S) as a model. Systematic modifications were made to arrive at a partially defined meridic diet for *C. capitata.* The rationale for using Srivastava diet (diet S) as a model was the similarity of dietary ingredients used in the mass rearing for both *B. dorsalis* and *C. capitata* at the USPBARC facility. Presumably, the nutritional needs for these two tephritids are similar.

Diet S, an agar gelled medium, originally developed by Srivastava et al. (1989) and Srivastava and Pant (1981) for *B. dorsalis* (Hendel) and *B. cucurbitae* (Coquillett), was tested for suitability on *C. capitata.* Larvae remained on the surface of the agar-gelled medium and did not survive. Larvae were able to survive after the replacement of agar with millfeed on diet S. Millfeed and casein in diet S possess overlapping amino acid compositions. The amino acid mixture from millfeed formula (Table 2) was selected, and that from casein was disregarded. Agar was used as a bulking agent. However, many attempts of using agar as a bulking agent proved unsuccessful with this formulation (Table 2). Agar was then replaced with corncob (30/80) (Mount Pulaski products, Chicago, IL) as the bulking agent. A meridic diet (*C. capitata* #1) containing corncob as a bulking agent, that supported larval development, was successfully formulated.

Larval Development on *C. capitata* #1 Diet. The tested parameters for larvae fed on *C. capitata* #1 diet were not significantly different from those fed on diet T (control) except that the new diet resulted in a ≈1.3-d delay in larval development period within the same generation (Table 3). The cause of this delay is unknown. Perhaps natural food is stimulatory and promotes feeding activity. Alternatively, the larvae may have difficulty in using nutrients that do not need to be digested. This delay in larval development period was reproduced over two subsequent generations (Table 3). However, larval development period of F_1 and F_2 were significantly shorter than the parent generation (P) in both control diet and *C. capitata* #1 diet; no differences between F_1 and F_2 were evident. Among generations, pupal weights from the F_1 and F_2 were heavier than the parent generation (P) (Table 3).

Nutritional Requirements. The deletion of the 10 essential amino acids (Table 2) from the *C. capitata* #1 diet resulted in no survivorship (Table 4). Removal of the eight non-essential amino acids (Table 2) delayed development ≈2.3 d and decreased pupal weight. However, total pupal recovery was not affected (Table 4). The omission of the 10 vitamins (Table 2) delayed larval development, decreased pupal recovery, pupal weight, adult emergence, and flight ability (Table 4). Larvae reared on *C. capitata* #1 diet lacking exogenous sugar not only delayed larval development but also reduced the pupal weight. Deletion of ribonucleic acid from the *C. capitata* #1 diet extended larval developmental period, whereas omitting cholesterol from the *C. capitata* #1 diet decreased the pupal recovery, pupal weight, adult emergence, and larval period. Salt mixture did not seem to have any developmental effects statistically (Table 4).

In the absence of the 10 essential amino acids (Table 4), larvae did not survive past the first instar. Nonessential amino acids may be required for improving normal growth and development by supporting the 10 essential amino acids and B-vitamins. Insect vitamin requirements vary with species, with most requiring thiamine, riboflavin, nicotinic acid, pyridoxine, and pantothenic acid (Friend and Patton 1956, Mitsuhashi 1998). Sugar, a source of carbohydrate, is necessary for normal growth and development of phytophagous insects, especially in terms of concentration (House 1962). Results of the current study agree with those of Achala-Paripurna and Srivastava (1989) that the ab-

Table 4. Effect of group nutrient deletion from *C. capitata* #1 diet on *C. capitata* development

Deleted items	Larval period, days	Pupal recovery, %	Pupal wt, mg	Adult emergence, %	Flier, %
Control (diet T)	7.65 ± 0.07e	92.00 ± 1.56a	9.96 ± 0.12a	96.50 ± 1.13a	61.44 ± 7.15a
None (*C. capitata* #1)	9.31 ± 0.06d	95.25 ± 0.75a	9.41 ± 0.09a	96.36 ± 1.09a	53.94 ± 5.46ab
10 essential amino acids	No survival	No survival	No survival	No survival	No survival
8 nonessential amino acids	11.61 ± 0.13b	85.00 ± 3.42a	8.43 ± 0.13b	91.10 ± 2.72ab	73.34 ± 1.76a
10 Vitamins	18.57 ± 0.44a	56.50 ± 2.36b	6.95 ± 0.19d	55.42 ± 10.35c	26.91 ± 5.91b
Sugar	11.03 ± 0.12b	81.50 ± 2.36a	7.60 ± 0.10c	93.76 ± 1.69a	37.77 ± 4.19ab
Salt mixture	9.28 ± 0.15d	80.50 ± 6.44a	9.94 ± 0.07a	94.39 ± 1.04a	52.32 ± 6.50ab
Cholesterol	9.37 ± 0.24d	38.00 ± 6.05b	8.69 ± 0.15b	78.91 ± 2.94b	46.76 ± 7.18ab
Ribonucleic acid	10.64 ± 0.22bc	85.50 ± 5.64a	9.60 ± 0.05a	91.73 ± 1.49a	44.16 ± 6.74ab
F value	219.84	18.41	75	18.75	3.14
df	40	40	40	40	40
P	<0.0001	<0.0001	<0.0001	<0.0001	0.0090

Means within a column followed by different letters were statistically different ($\alpha = 0.05$, ANOVA test).

sence of 2,000 mg sugar in the 50 g of diet resulted in pupae weight loss and slow larval development. Fatty acids, especially the polyunsaturated group, have been shown to be an essential requirement for many insects (Kanthi and Pant 1988). Cholesterol alone without interaction with fatty acids was shown to be important for pupal formation in this study and agrees with the findings of Kanthi and Pant (1988). The absence of ribonucleic acid, a protein source, in the diet produced a delay in development. Further studies are needed to quantify the specific nutrient requirements for *C. capitata.*

The *C. capitata* #1 larval diet reported here is a meridic diet because it contains one natural ingredient (with unknown chemical structures)—corncob (Dougherty 1959). However, this diet possesses a "holidic diet" quality, because corncob is a nutritionally inert substance. Although corncob contains trace amounts of nutrients (1 gram of corncob contains 0.90 IU vitamin A, 0.0005 mg carotene, 0.00002 mg biotin, 0.0068 mg niacin, 0.0025 mg pantothenic acid, 0.0031 mg pyridoxine, 0.0011 mg riboflavin [Andersons, Maumee, OH], 1.3 mg alanine, 0.5 mg arginine, 1.3 mg aspartic acid, 1.8 mg glutamic acid, 0.8 mg glycine, 0.2 mg histidine, 0.4 mg isoleucine, 1.4 mg leucine, 0.5 mg lysine, 0.5 mg phenylalanine, 0.7 mg serine, 0.4 mg threonine, and 0.4 mg tyrosine), it may lack certain essential nutrients for *C. capitata* (C.L. Chang and H. Ako, unpublished data). This finding together with the results from amino acid deletion from #1 diet confirmed that larvae of *C. capitata* were not able to survive on the diet containing only corncob and water owing to the lack of certain essential amino acids.

In conclusion, *C. capitata* #1 diet is the first chemical-based diet containing corncob as a bulking agent (i.e., meridic diet). The meridic *C. capitata* #1 diet described here is not necessarily the most nutritious diet for *C. capitata* larvae. It is, however, a base-line diet that would support the larval development of *C. capitata* as well as the diet currently used in mass-rearing facilities. The high cost of this meridic diet at this time (about $2,000 per million pupae) prohibits a direct substitute for the mass-rearing diet. However, it does provide nutritional data upon which further nutritional studies can be based.

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